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A COMPARATIVE DEMOGRAPHY OF PLANTS BASED UPON ELASTICITIES OF VITAL RATES

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Abstract. Elasticities of matrix elements from population projection matrices are commonly used to analyze the relative contributions of different life history transitions (birth, survival, growth) to the finite rate of increase (λ). Hitherto, comparative demography based on matrix models has relied upon decomposing elasticity matrices into blocks, each containing matrix elements deemed to represent recruitment, stasis, or progression to larger size classes. Elasticities across an entire matrix always sum to unity, and different populations and species can be compared on the basis of the relative proportions of these three variables. This method has been widely used, but it contains a weakness in that the value of matrix elements is a function of more than one vital rate. For example, transitions representing progression to larger size classes involve a survival rate as well as a growth rate. Ideally, then, demographic comparisons between populations should be made using elasticities of vital rates themselves, rather than elasticities of matrix elements that are compounds of those rates. Here, we employ the complete set of general equations for the elasticity of vital rates in an entirely new analysis of matrices for 102 species of perennial plants. The results show a surprising similarity to an earlier analysis based upon matrix element elasticity and provide important confirmation of general patterns of correlation between plant life history and demography. In addition, we show that individual vital rate elasticities cannot, on their own, predict variation in life history. Therefore, all three demographic processes (survival, growth, and reproduction) are necessary to account for life history variation. The new analysis provides a firmer foundation for comparative demography.

Key words: age at first reproduction; damping ratio; demographic triangle; elasticity analysis; finite rate of increase; generation time; longevity; net reproductive rate; perennial plants; period of oscillation; population projection matrix.

INTRODUCTION

Comparative biology seeks to uncover the fundamental variables that lie hidden within the rich variety of form and life history found among living species and to discern their influence in shaping this variation. In the field of demography, the fundamental variables are the age- or stage-specific vital rates of survival, growth, and fecundity and the theory applying to structured populations is very well developed. Though the fundamental variables are clearly identified, the distribution of living populations in the space defined by these parameters is less well understood. This is a solvable problem because there now exists a substantial data set of matrix models for plant populations based upon stage- or size-specific vital rates measured in the field. This type of model is a singularly appropriate tool for the analysis of the complex life cycles typical of perennial plants and provides a sound basis for comparative analysis (Caswell 2001).

Hitherto, comparative demography based on matrix models has relied upon decomposing an elasticity matrix (de Kroon et al. 1986) for each population into three components, one each for the matrix elements representing recruitment, stasis (survival with no change in size class), and progression to larger size classes. The elasticity value for a particular matrix element measures the effect on the finite rate of increase (λ) of small perturbations to the corresponding transition in the life cycle. Since elasticities across an entire matrix always sum to unity, different populations can be compared on the basis of the relative proportions of these three components. Using this method, Silvertown et al. (1993) found that semelparous perennial herbs, iteroparous herbs, and woody plants each tended to occupy a different region of the parameter space defined by the three components. Among iteroparous herbs, there was also a difference between species of forest and open habitats. Subsequent studies of species not included in the dataset analyzed by Silvertown et al. (1993) have tended to confirm the original patterns (e.g., Bullock et al. 1994, Floyd and Ranker 1998).

Silvertown and Franco (1993) used the same technique for intraspecific comparisons between herb pop-

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ulations exposed to different intensities of burning or grazing and found that these environmental treatments moved populations in a consistent manner within their appropriate segment of elasticity space. In addition, data from Durán and Franco (1992) analyzed by Silvertown and Franco (1993) showed that populations of the palm *Pseudophoenix sargentii* growing along a successional gradient moved in a consistent manner within the tree region of elasticity space. When the intraspecific trajectories for the different species were assembled on common axes, they suggested a general tendency for succession to move populations along an arc in elasticity space, starting with relatively high values of recruitment in early succession, passing through a region with high values of progression in mid succession, and terminating at a values of stasis equal to one (Silvertown and Franco 1993). In general, a population at equilibrium ($\lambda = 1$) occupies a defined position in elasticity space determined by life history traits, particularly longevity, and ecological factors such as density or disturbance that impact upon λ displace populations from this point (Oostermeijer et al. 1996, Silvertown et al. 1996, Valverde and Silvertown 1998, Silva Matos et al. 1999).

Though the elasticity of matrix coefficients has proved to be useful for interspecific and intraspecific comparisons, they do not cleanly separate the contributions of fecundity, growth, and survival to λ because every matrix element is a function of more than one vital rate. For example (see Eq. 4 below), recruitment is the product of the survival of reproductive adults and their fecundity. Similarly, transitions represented by progression (Eq. 2 below) involve a survival rate as well as a growth rate that causes individuals to graduate between classes. Ideally, demographic comparisons between populations should be made using elasticities of vital rates themselves, rather than for matrix elements that are compounds of those rates.

In addition, matrix element elasticities appear to be sensitive to the definition and number of size classes used in matrix construction and this may potentially create artifacts in comparisons between species (Enright et al. 1995). In models of two tropical tree species Zuidema and Zagt (in Zuidema 2000) found that greatly increasing the number of size categories significantly changed the elasticities of matrix elements, but left vital rate elasticities almost unaltered. Thus, interspecific comparisons between species, which inevitably involve comparing matrix models that differ in their construction, will be less prone to error if they are based upon vital rate elasticities.

Formulae for the elasticities of survival and growth were given by Caswell (1989), to which Zuidema and Franco (2001) added formulae for negative growth and fecundity. Here, we complete the set of general equations for the elasticity of vital rates, applicable to all plant life cycles including those with clonal growth.

We then use these formulae in an entirely new analysis of matrices for 102 species of perennial plants.

The questions we ask are: Are there regularities in how species ordinate in a parameter space defined by the elasticities of vital rates? Are these patterns different from those found by Silvertown et al. (1993) which were based upon matrix element elasticities? How do other population parameters, e.g., generation time (τ), and rates of increase (r , λ , R_0) vary within elasticity space? Do these patterns have a biological (as distinct from a purely mathematical) interpretation? What are the ecological and evolutionary implications of the patterns?

METHODS

Calculation of vital rate elasticities

Unlike the elasticity of matrix elements, the elasticity of the underlying vital rates effectively separates the independent influence of the three demographic processes on population growth. Stage-based, Lefkovich matrix models contain up to six different kinds of element: recruitment of seeds (to the seed bank; F_1), recruitment of seedlings (from either the seed bank or from recently produced seeds; F_2), recruitment of ramets (through clonal growth; C), stasis (P), progression (positive growth; G), and retrogression (negative growth; R). These elements denote contributions from one stage class, say j , to another, say i , and are therefore represented as F_{ij} , C_{ij} , P_j , G_{ij} , and R_{ij} . They are the result of combinations of basic processes, namely survival in a given stage class (σ_j), positive growth (γ_{ij}), negative growth (ρ_{ij}), individual ramet production (κ_{ij}), and individual fecundity (ϕ_{ij} ; including either F_1 or F_2). Although the exact formulae for the calculation of matrix elements may vary from study to study (e.g., birth-flow vs. birth-pulse populations; see Caswell 2001), we can fairly assume that, because most perennial plants reproduce seasonally, most authors used the birth-pulse population formulas:

$$P_j = \sigma_j \left(1 - \sum \gamma_{ij} - \sum \rho_{ij} \right) \quad (1)$$

$$G_{ij} = \sigma_j \gamma_{ij} \quad (2)$$

$$R_{ij} = \sigma_j \rho_{ij} \quad (3)$$

$$F_{ij} = \sigma_j \phi_{ij} \quad (4)$$

$$C_{ij} = \sigma_j \kappa_{ij}. \quad (5)$$

Given a demographic matrix with an accurate description of the position of each of these elements and assuming the authors actually calculated them according to these formulas, it is possible to calculate the values of the vital rates implicit in each cell of the matrix. Once these five vital rates have been identified and isolated, their corresponding elasticity (E) can also be calculated. Caswell (2001:237) has conjectured that the elasticities of vital rates would not work as a tool to classify life histories because λ , the population

growth rate, is a homogeneous function of degree 2 of all vital rates and, therefore, their elasticities must add up to a value of 2. Indeed, as we found (see *Results*) and as Caswell mentions in the same page, λ is a homogeneous function of degree 1 of survival and their elasticity adds up to 1. Intuitively, this makes sense because survival is present in all positive matrix elements. This, however, is not the case with any of the other vital rates, which appear in some, but not all, cells with positive values. For example, both fecundity and clonal growth are open-ended processes that can vary from zero to (at least in theory) infinity. There is also no restriction as to where in the life cycle fecundity and clonal growth can occur, i.e., they may occur everywhere or nowhere at all. Similarly, regardless of their contribution to stasis, there is no restriction as to the values that positive and negative growth can have. They depend on the (usually arbitrarily defined) stage duration (Caswell 2001, section 6.4). All this seems to account for the empirical fact, found in the analyses presented here, that, with the exception of survival, the combined elasticities of all other vital rates do not exceed unity. They do, however, seem to be bounded by this value, restricting the total sum of elasticities to vary between 1, when survival dominates, and 2, as other processes gain importance.

Although we have five different vital rates (σ_j , γ_{ij} , ρ_{ij} , ϕ_{ij} , and κ_{ij}), positive, negative, and clonal growth can all be ascribed to one process, i.e., growth. Therefore $E_{\text{survival}}(E_{\sigma} = \Sigma e_{\sigma})$, $E_{\text{growth}}(E_{\gamma} + E_{\rho} + E_{\kappa} = \Sigma |e_{\gamma}| + \Sigma |e_{\rho}| + \Sigma |e_{\kappa}|)$; see the last paragraph in this subsection for the reason we add the absolute values of positive and negative growth), and $E_{\text{fecundity}}(E_{\phi} = \Sigma e_{\phi})$ within each species. Because λ is a homogeneous function of degree 1 of σ , the total sum of the elasticity values for survival is equal to 1 ($E_{\sigma} = 1$). This, however, does not mean we can only compare the elasticity values of the remaining vital rates. Just as we can standardize a series of values such that one of them is always equal to a constant, we can also calculate their proportional values. This we did (E_{survival}/E , E_{growth}/E and $E_{\text{fecundity}}/E$, where $E = E_{\sigma} + E_{\gamma} + E_{\rho} + E_{\kappa} + E_{\phi}$) and subsequently plotted the proportional elasticity values in triangular “elasticity space.” For simplicity, we labeled these axes S ($=E_{\text{survival}}/E$), G ($=E_{\text{growth}}/E$), and F ($=E_{\text{fecundity}}/E$).

The sensitivity s_{ij} of λ to changes in a matrix element a_{ij} is defined and calculated as follows (Caswell 1978):

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\mathbf{v} \cdot \mathbf{w}} \quad (6)$$

where a_{ij} corresponds to each of the elements defined in Eqs. 1–5, v_i and w_j are the corresponding elements of the left (\mathbf{v}) and right (\mathbf{w}) eigenvectors associated with λ , and $\mathbf{v} \cdot \mathbf{w}$ is their scalar product. The elasticities of λ to changes in the vital rates implicit in the matrix elements will be as follows (Caswell 1989 and 2001, Zuidema and Franco 2001).

survival:

$$\begin{aligned} e_{\sigma_j} &= \frac{\sigma_j}{\lambda} \frac{\partial \lambda}{\partial \sigma_j} \\ &= \frac{\sigma_j}{\lambda} \left[\frac{\partial \lambda}{\partial P_j} \frac{\partial P_j}{\partial \sigma_j} + \sum_i \frac{\partial \lambda}{\partial G_{ij}} \frac{\partial G_{ij}}{\partial \sigma_j} + \sum_i \frac{\partial \lambda}{\partial R_{ij}} \frac{\partial R_{ij}}{\partial \sigma_j} \right. \\ &\quad \left. + \sum_i \frac{\partial \lambda}{\partial F_{ij}} \frac{\partial F_{ij}}{\partial \sigma_j} \right] \\ &= \frac{\sigma_j}{\lambda} \left[s_{jj} \left(1 - \sum_i \gamma_{ij} - \sum_i \rho_{ij} \right) + \sum_i s_{ij} \gamma_{ij} \right. \\ &\quad \left. + \sum_i s_{ij} \rho_{ij} + \sum_i s_{ij} \phi_{ij} \right] \end{aligned} \quad (7)$$

positive growth ($i > j$):

$$\begin{aligned} e_{\gamma_{ij}} &= \frac{\gamma_{ij}}{\lambda} \frac{\partial \lambda}{\partial \gamma_{ij}} = \frac{\gamma_{ij}}{\lambda} \left(\frac{\partial \lambda}{\partial P_j} \frac{\partial P_j}{\partial \gamma_{ij}} + \frac{\partial \lambda}{\partial G_{ij}} \frac{\partial G_{ij}}{\partial \gamma_{ij}} \right) \\ &= \frac{\gamma_{ij}}{\lambda} [s_{jj}(-\sigma_j) + s_{ij} \sigma_j] \end{aligned} \quad (8)$$

negative growth ($i < j$):

$$\begin{aligned} e_{\rho_{ij}} &= \frac{\rho_{ij}}{\lambda} \frac{\partial \lambda}{\partial \rho_{ij}} = \frac{\rho_{ij}}{\lambda} \left(\frac{\partial \lambda}{\partial P_j} \frac{\partial P_j}{\partial \rho_{ij}} + \frac{\partial \lambda}{\partial R_{ij}} \frac{\partial R_{ij}}{\partial \rho_{ij}} \right) \\ &= \frac{\rho_{ij}}{\lambda} [s_{jj}(-\sigma_j) + s_{ij} \sigma_j] \end{aligned} \quad (9)$$

fecundity:

$$e_{\phi_{ij}} = \frac{\phi_{ij}}{\lambda} \frac{\partial \lambda}{\partial \phi_{ij}} = \frac{\phi_{ij}}{\lambda} \left(\frac{\partial \lambda}{\partial F_{ij}} \frac{\partial F_{ij}}{\partial \phi_{ij}} \right) = \frac{\phi_{ij}}{\lambda} (s_{ij} \sigma_j) \quad (10)$$

clonal growth:

$$e_{\kappa_{ij}} = \frac{\kappa_{ij}}{\lambda} \frac{\partial \lambda}{\partial \kappa_{ij}} = \frac{\kappa_{ij}}{\lambda} \left(\frac{\partial \lambda}{\partial C_{ij}} \frac{\partial C_{ij}}{\partial \kappa_{ij}} \right) = \frac{\kappa_{ij}}{\lambda} (s_{ij} \sigma_j). \quad (11)$$

Notice that because σ_j appears with both a positive and a negative sign in the equations for the elasticity of positive and negative growth, these elasticities can acquire either a positive or a negative value. This obviously depends on the relative value of the sensitivity elements associated with them. These, in turn, depend on the relative reproductive values of the categories involved. Thus, moving to a category with a lower reproductive value implies a negative effect on population growth rate, while moving to a category with a higher reproductive value results in a positive value of elasticity (Caswell 2001:220). Because we were interested in the magnitude of the changes and not in their sign, we added the absolute values of the elasticities of these vital rates.

The data set

Demographic data in the form of matrix models were collected from the literature. More than 120 species were identified. However, particularly for species with

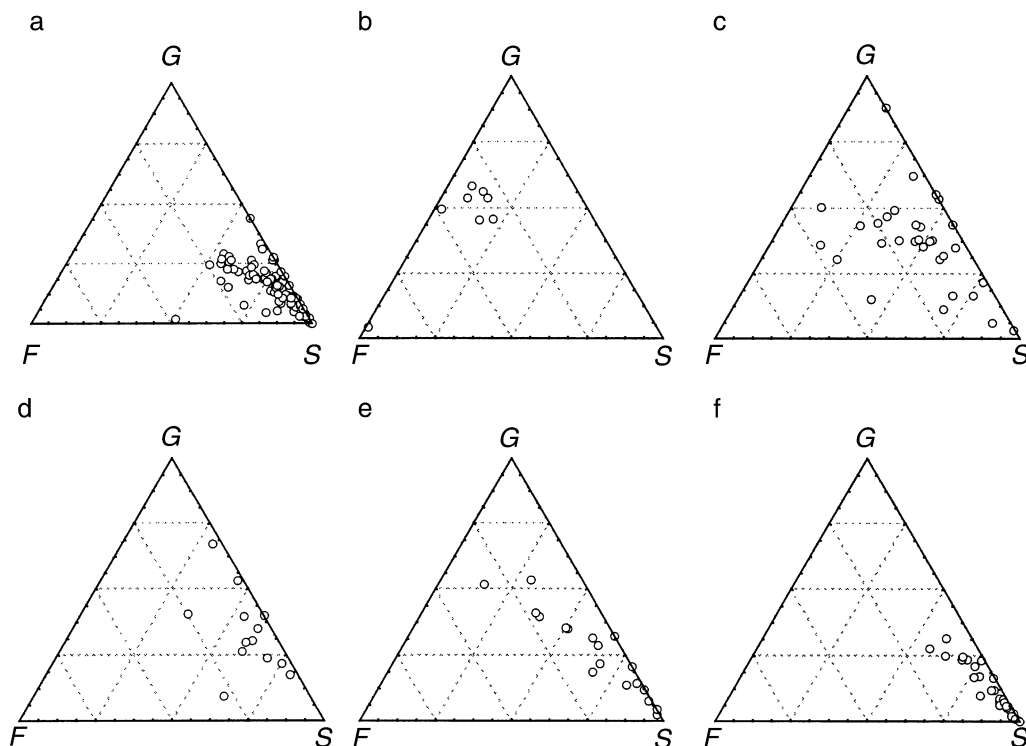


FIG. 1. The distribution of 102 species of perennial plants in elasticity space, as defined by the vital rates survival (S), growth (G), and fecundity (F). (a) Distribution of proportional values of elasticity. (b)–(f) Rescaled elasticity values for each of five groups of plants: (b) semelparous plants, (c) iteroparous herbs from open habitats, (d) iteroparous forest herbs, (e) shrubs, and (f) trees.

complex life cycles, not all of the papers contained enough information to decompose the matrix data into their component vital rates. Therefore, although we incorporated a substantial number of new studies, we had to drop some of the species presented in previous analyses (e.g., Franco and Silvertown 1996). The results presented here come from 102 species listed in the Appendix. Projection analyses were conducted with the program STAGECOACH (Cochran and Ellner 1992). This program was also used to calculate other life history variables as in Franco and Silvertown (1996). The intrinsic rate of increase (r) was calculated as the natural logarithm of λ , the dominant eigenvalue of the population matrix for each species. Life span (L) is the expected age at death, conditional on passing through stage 1 (Cochran and Ellner's Eq. 6). Age at sexual maturity (α) is the average age at which an individual enters a stage class with positive fecundity (Cochran and Ellner's Eq. 15). Two measures of generation time, \bar{A} , the mean age of parents of offspring produced at stable stage distribution (Cochran and Ellner's Eq. 26), and μ , the mean age at which members of a cohort produce offspring (Cochran and Ellner's Eq. 27), were calculated. This was done because they measure slightly different things, but also because values for some species were computable by one measure and not the other. Finally, the net reproductive rate (R_0) is the av-

erage number of offspring produced by an individual over its life span (Cochran and Ellner's Eq. 18). In cases where more than one type of recruit occurred (i.e., in species with clonal growth), all these life history indices were taken for the average "newborn equivalent," as weighted by the relative reproductive value of the different types of offspring in STAGECOACH (Cochran and Ellner 1992). Additionally, using the spectrum of eigenvalues for each matrix (species) we calculated the damping ratio (ρ), a measure of the speed with which the population converges to stability, and the period of oscillation (P_i , where i corresponded to the highest possible complex eigenvalue), the average duration of an oscillation as the population converges to equilibrium. These correspond to equations 4.90 and 4.99 of Caswell (2001). Not all matrices yielded complex eigenvalues, and therefore some species lack P_i .

In order to gain some insight as to the variation in life histories in elasticity space, we fitted contour surfaces to the life history variables plotted as a fourth axis on the triangle. We chose the "special cubic smooth" of Statistica (StatSoft 2000). This model has the form $y = b_1x_1 + b_2x_2 + b_3x_3 + b_{12}x_1x_2 + b_{13}x_1x_3 + b_{23}x_2x_3 + b_{123}x_1x_2x_3$, where y is the life history variable plotted on the fourth axis, $x_1 = F$, $x_2 = S$, and $x_3 = G$. This fitting procedure was applied to the rescaled elas-

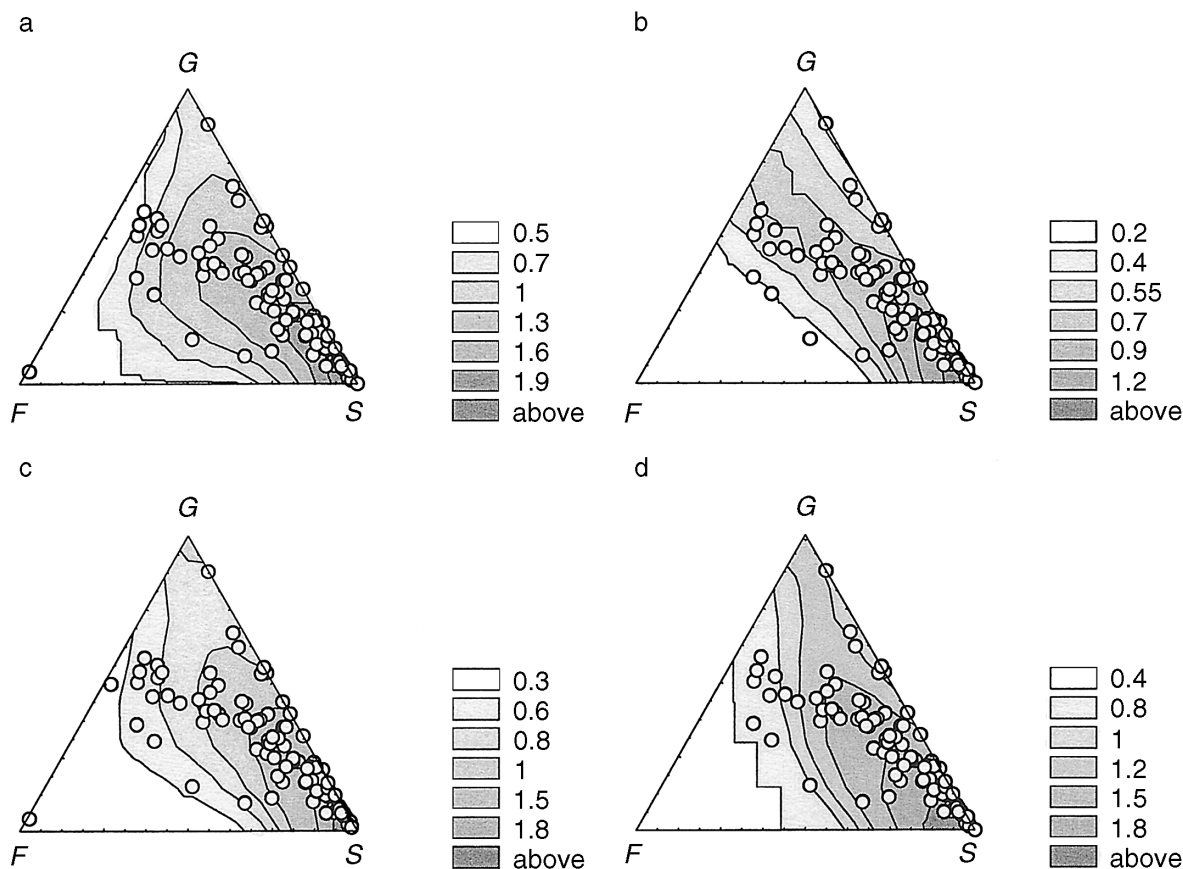


FIG. 2. Variation of age-related life history variables of 102 species of perennial plants in elasticity space: (a) average life span; (b) age at sexual maturity; (c) generation time, \bar{A} ; (d) generation time, μ . All four dependent variables are log transformed (original units were years).

ticities (see *Results*). Rather than fitting the best possible model, our purpose here was to obtain overall patterns of variation of life history variables in elasticity space. All regressions were significant ($P < 0.001$), but different elements of the model contributed in different degrees (significance) to individual life history variables. Despite this, we decided to retain the full model for all life history variables investigated. Except in the case of the intrinsic rate of increase and the damping ratio, all life history variables were logarithmically transformed before fitting.

RESULTS

The distribution of species in vital rate (proportional) elasticity space (Fig. 1a) occupied only one-quarter of the whole triangle because S comprised between 50% and 100% of total elasticity in all species. To facilitate comparison with the earlier triangular plot of matrix elasticities obtained by Silvertown et al. (1993), we rescaled the axes of the quarter triangle so that elasticities mapped onto themselves as $S \equiv 2S - 1$, $G \equiv 2G$ and $F \equiv 2F$. In the rescaled figures, short-lived, semelparous perennials occurred along the G axis (Fig. 1b), iteroparous herbs of open habitats appeared scat-

tered in the center of the triangle (Fig. 1c), iteroparous forest herbs were found along the S axis (Fig. 1d), shrubs spanned a long arc from the center of the triangle to the S vertex (Fig. 1e), and trees tended to concentrate toward the S vertex (Fig. 1f).

Life span, age at sexual maturity, and generation time exhibited similar topographies within elasticity space (Fig. 2a–d). In general, these attributes increased from the G and F corners of the triangle toward the S corner. That is, plants that live longer, reproduce at a later age, and have longer generation times had higher survival elasticities. Age at sexual maturity showed a slight increase near the F – G axis (Fig. 2b). The two measures of generation time showed similar patterns of variation in elasticity space (Fig. 2c, and d).

The dynamic properties of the populations analyzed also followed clear patterns in elasticity space (Fig. 3). The intrinsic rate of increase rose in all directions from near its equilibrium value ($r = 0$) at the S vertex (Fig. 3a). The maxima, however, were not at the G and F vertices, but between them where semelparous perennials tend to be found. The damping ratio, however, did have maxima at the G and F vertices (Fig. 3b). The period of oscillation decreased from the S vertex toward

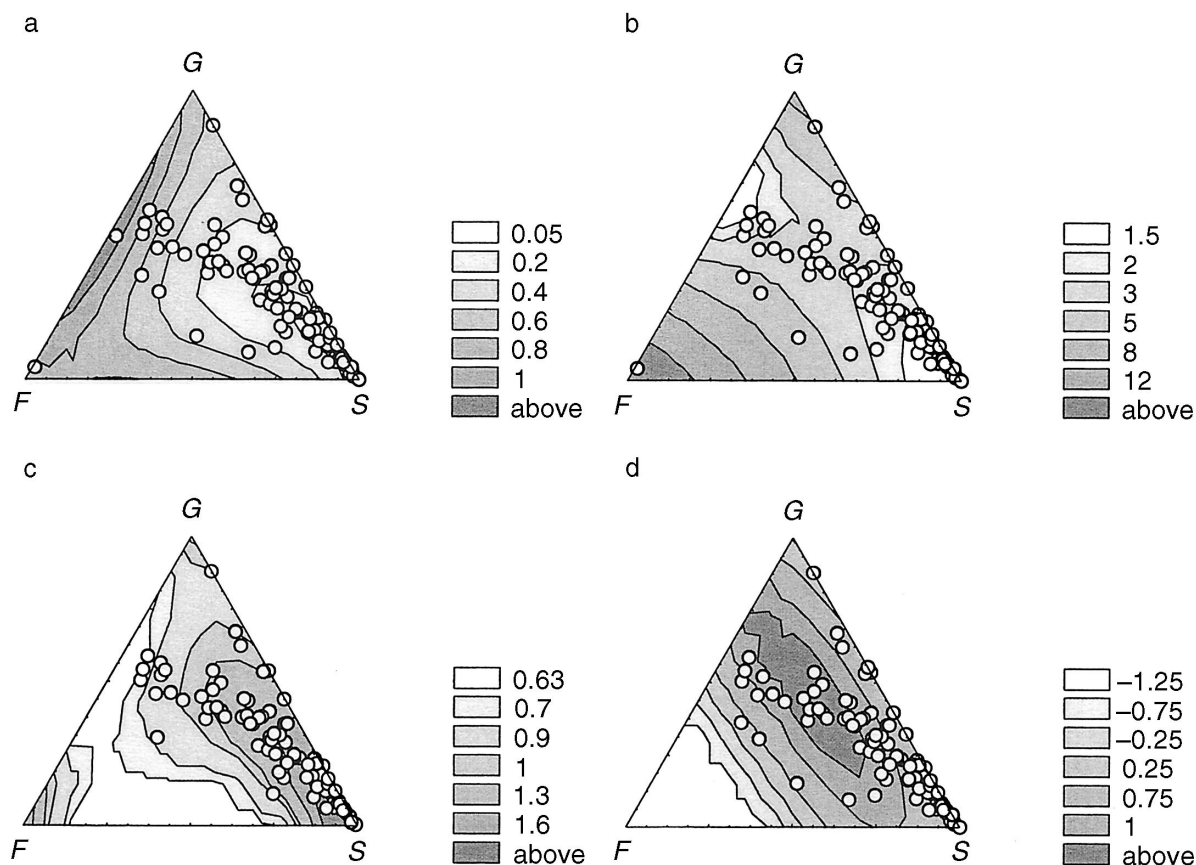


FIG. 3. Variation in the value of demographic parameters of 102 species in elasticity space: (a) intrinsic rate of increase (yr^{-1}); (b) damping ratio (dimensionless); (c) period of oscillation (yr); (d) net reproductive rate (newborns per life span). Dependent variables in (c) and (d) were log transformed.

the area occupied by semelparous herbs (Fig. 3c). It was not, however, as small near the G vertex and seemed to increase toward the F vertex. Unfortunately, the matrix for *Linum catharticum*, the only species near the F vertex of the triangle, failed to produce an estimate of the period of oscillation. It was therefore difficult to judge how reliable the trend toward this vertex is. Finally, the net reproductive rate decreased from a peak near the center of the triangle, where herbs and shrubs of open or disturbed habitats were located, toward all three vertices of the triangle (Fig. 3d). Once

again, however, it was impossible to assess whether the trend toward the F corner was an unrealistic extrapolation. Finally, the life history attributes studied tended to be correlated with each other, but there were some exceptions (Table 1).

DISCUSSION

Elasticities of vital rates vs. matrix element elasticities

The distributions of species grouped by life history and habitat plotted in (rescaled) vital-rate elasticity

TABLE 1. Spearman rank correlation coefficients between pairs of life history attributes.

Attribute	ρ	$\log P_i$	$\log L$	$\log \alpha$	$\log R_0$	$\log \tilde{A}$	$\log \mu$
r	0.322 (101)	-0.330 (85)	-0.226 (100)	-0.257 (95)	0.762 (96)	-0.604 (99)	-0.178 (96)
ρ		-0.699 (85)	-0.686 (100)	-0.680 (95)	-0.044 (96)	-0.684 (98)	-0.667 (96)
$\log P_i$			0.781 (84)	0.662 (80)	0.054 (81)	0.759 (84)	0.706 (81)
$\log L$				0.756 (95)	0.254 (96)	0.852 (98)	0.956 (96)
$\log \alpha$					0.162 (95)	0.751 (93)	0.733 (95)
$\log R_0$						-0.152 (94)	0.328 (96)
$\log \tilde{A}$							0.799 (94)

Notes: Because not all attributes could be calculated for all species, sample size (in parentheses; missing data pairwise deleted) ≤ 102 . Figures in bold are significant at the 1% level; coefficients in italics are statistically significant at the 5% level.

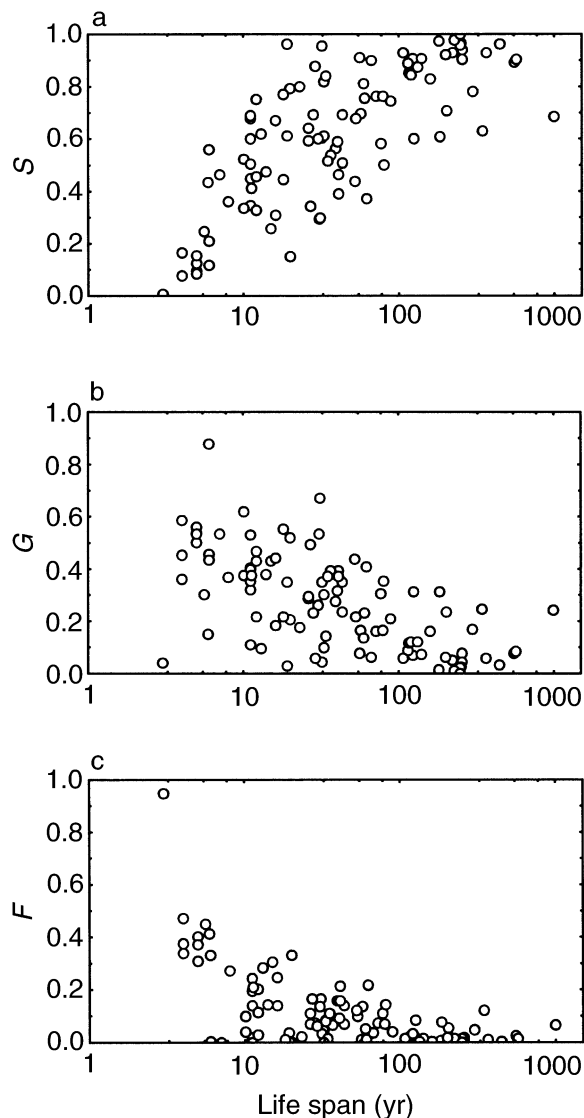


FIG. 4. The relationship between each of the elasticities of (a) survival, (b) growth, and (c) fecundity and life span for 102 species of perennial plants.

space (Fig. 1b–f) are all remarkably similar to the original distributions of the groups plotted using matrix element elasticities by Silvertown et al. (1993). The match between the two analyses is all the more remarkable because only 52 species out of the total of 120 analyzed so far were present in both the original dataset and the current one, and four of these have new data (see the Appendix). The similarity of the two sets of distributions demonstrates that, although matrix elasticities are technically compounds of vital rates, the matrix regions that were originally designated as representing growth, stasis, and fecundity were appropriately named for practical purposes. It is evident from this that the elasticities of distinct matrix regions, as defined by Silvertown et al. (1993), are largely determined by contributions from specific vital rates.

Notwithstanding the agreement between element and vital rate elasticities, the latter are to be preferred because they strictly correspond to the fundamental demographic processes that matrix element elasticities only approximate. Another reason for the preference is that matrix element elasticities are influenced by the number and breadth of size classes used in a population model (Enright et al. 1995), while vital rate elasticities are more robust to such details of matrix construction. As mentioned in *Introduction*, Zuidema and Zagt (in Zuidema 2000) found that, in contrast to the elasticity of matrix elements, the elasticity of vital rates was rather insensitive to changes in the number of categories (matrix size) employed.

It is important to bear in mind that whichever type of elasticity analysis is used, estimates of demographic parameters will always be highly dependent upon the ecological conditions, for example the successional status, under which the estimates were obtained (Silvertown et al. 1996, Silva Matos et al. 1999). This problem suggests that standardization may be useful before species are compared. One possible method of standardization would be to confine comparisons only to those species represented by populations at equilibrium (i.e., $\lambda \approx 1$ or $r \approx 0$). However, this would ignore the fact that equilibrium is not a typical state for the populations of some species, particularly short-lived ones, and such a comparison would therefore be biased against certain life history types. In the present data set, only 44 of the 102 species fall within the bounds $0.95 < \lambda < 1.05$ and these are mainly woody (nine shrubs and 20 trees). Standardization by this method would severely bias the data set and defeat the object of comparing species by excluding all eight semelparous perennial species, most (22 out of 31 species) iteroparous herbs of open habitats, and half the forest herbs and shrubs (seven out of 13 and nine out of 18 species, respectively).

Correlates of vital rate elasticities

As is to be expected, elasticities of vital rates correlate with life history and population parameters. Longevity, age at first reproduction, and generation time all increase along an arc that runs from the F vertex to the S vertex, passing through the center of the triangle (Fig. 2a–d). These patterns reflect the changes in plant life history that occur with succession from pioneer to climax communities (Silvertown and Franco 1993). Population model properties also correlate with vital rate elasticities, but in a more varied manner. The intrinsic rate of natural increase (r) is highest at the point $F \approx G \approx 0.5$, $S = 0$ and decreases toward $S = 1$ (Fig. 3a). By contrast, the net reproductive rate (R_0) is highest near the center of the triangle (Fig. 3d). The damping ratio (ρ), which measures how quickly a population's size structure converges on equilibrium, is high for short-lived species at the G and F vertices and decreases toward the center of the triangle and the S vertex. (Fig. 3b). The period of oscillation is lowest

near the center of the triangle and toward the *G* vertex and increases toward the *F* and *S* vertices (Fig. 3c).

The patterns shown in Fig. 3 are more complex than one would expect if the variety of life histories among the 102 species could be reduced to one-dimensional classifications of the *r*-*K* (MacArthur and Wilson 1967) or fast-slow (e.g., Promislow and Harvey 1990) type. If a single axis completely captured life history variation, the contours in elasticity space would be identical for different variables (if parameters were perfectly and positively correlated), or exact inverses of each other, with "valleys" in one attribute corresponding to "hills" in another (if parameters were negatively correlated). This not being the case accounts for the weak or insignificant correlation among some life history attributes (Table 1). Similarly, the relationship between the elasticity of a particular vital rate and individual life history parameters is not a function in the mathematical sense (Fig. 4). Although a few points in a graph of this type may give the impression that some attributes are correlated with elasticity, the number of species analyzed here shows that these relationships are represented by "triangular clouds," not by functions varying in a particular direction. The boundary confining these points, however, does follow a particular increasing (*S*) or decreasing (*G* and *F*) function. These patterns of variation occur in other life history parameters studied here and lead to the conclusion that all three vital rates are needed to account for variation in life history.

The failure of models such as *r* and *K* to account for the variety of life histories has prompted Stearns (1992) to conclude that "we may have to reconcile ourselves to dealing with sets of patterns rather than single patterns." Our results offer a less gloomy prospect, and suggest that the demographic triangle based upon vital rate elasticities does provide a general pattern that links life history, demography, and community-level processes such as succession.

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APPENDIX

The data set of species employed in the analysis of the elasticity of population growth rate to changes in vital rates is available in ESA's Electronic Data Archive: *Ecological Archives* E085-012-A1.